

VEGETATIVE AND SEXUAL REPRODUCTION IN
THE RARE SEDGE, *CAREX POLYMORPHA*
(CYPERACEAE)

LISA A. STANDLEY AND JUDITH L. DUDLEY

ABSTRACT

Carex polymorpha is a rare sedge of eastern North America, currently a candidate for Federal listing. Populations in Maine and Massachusetts were studied to establish a scientific basis for population monitoring, management, and protection. We examined potential and actual fecundity, and used pollination experiments to test hypotheses regarding breeding systems. Sexual reproductive characters were compared with the common species, *C. vestita*. Studies of vegetative reproduction of *C. polymorpha* included determination of rhizome growth patterns, above- and below-ground biomass, organ dimensions and dynamics of shoots in permanent plots.

Both vegetative growth and sexual reproduction appear to be correlated with canopy closure. Numbers of flowering shoots, flowers and seeds appear to be limited by light availability. Both the number of achenes and the percent seed set per flowering shoot are similar in *Carex polymorpha* and *C. vestita*. Density of vegetative shoots and of leaf and rhizome sizes are also correlated with canopy cover: biomass production appears to be limited by light levels. Shoot dynamics are correlated with light and microhabitat type. The least stable shoot populations are in disturbed, open sand sites, while shoot populations in undisturbed, open canopy sites have high turnover rates but stable sizes. These results suggest that canopy management may be critical to maintenance of vegetative and sexual reproduction in established populations of *Carex polymorpha*.

Key Words: *Carex*, rare species, reproductive biology, vegetative reproduction, Maine, Massachusetts

INTRODUCTION

Carex polymorpha Muhl. (section *Paniceae* G. Don) is a rare sedge with fewer than 30 extant populations distributed from Maine to West Virginia. It is listed as rare in each of the states in which it is known to occur or to have occurred. *Carex polymorpha* has been under review by the U.S. Fish and Wildlife Service for Federal listing since 1983 when it was placed in category 2, comprised of those taxa for which listing may be appropriate, but for which substantial data on biological vulnerability and threats are needed to ascertain their status. The primary goals of this study were to provide data on the life history and population dynamics of this rare sedge that would be of value in efforts

to monitor populations and to develop recommendations for management and protection strategies.

Section *Paniceae* G. Don is a group of approximately 12 *Carex* species of Eurasia and North America. In North America this section includes the European adventive *Carex panicea* L. and several widely distributed species of neutral or calcareous habitats that are, however, listed as rare in several states (*C. livida* (Wahl.) Willd., WA, NY; *C. meadii* Dewey, NY; *C. tetanica* Schkuhr., IA; *C. vaginata* Boott, NY; *C. woodii* Dewey, IA). Other species included in section *Paniceae* are *C. biltmoreana* Mackenz., a rare southern Appalachian endemic of wet shaded cliffs in the Blue Ridge Mountains and also under consideration for Federal listing; *C. chapmanii* Steud., a coastal plain endemic occurring from Florida to North Carolina; and *C. californica* L. H. Bailey, a rare species occurring from northwestern California to Idaho. *Carex californica* appears to be the closest relative of *C. polymorpha*. It is morphologically very similar in all vegetative and most floral characters, and differs only in the shorter and non-oblique beak of the perigynium.

Preliminary observations of populations of *Carex polymorpha* in Maine, Massachusetts, New Hampshire, Rhode Island, and Pennsylvania led us to develop the hypothesis that variation in flowering, seed set and vegetative growth is correlated with canopy cover. To test these hypotheses, field observations of plants and experimental manipulations were performed at two sites in Maine and one in Massachusetts. Permanent plots were established to study shoot life history, density and turnover of shoots. Destructive sampling of additional plots provided data on vegetative growth patterns, meristem dynamics, and vegetative morphology. We estimated light levels using photographs to quantify canopy cover and compared canopy cover in areas which had, or lacked, flowering shoots.

Observations also suggested that recruitment via sexual reproduction is limited, and that vegetative reproduction may be the most important factor in maintenance of existing populations. To characterize reproductive biology in *Carex polymorpha*, we observed flowering phenology and dichogamy, and investigated fecundity, seed set, and breeding systems. Sutherland (1986) investigated correlations among environmental and life-history characteristics and fruit set in plants. He found that fruit set is

always less than 100%, and attributed this reduction to pollinator limitation, lack of pollinator attraction, overproduction of flowers to compensate for variations in resource availability ("bet-hedging"), or selective abortion of embryos. We attempted to determine whether reduced seed set in *Carex polymorpha* was due to self-incompatibility, reduced pollen loads due to low air flows in shaded or brushy sites, or to "bet-hedging" and limited environmental resources by conducting experiments with controlled pollinations and comparing these results to open-pollinated plants in several habitats.

The final hypothesis tested was whether limited seed output is correlated with rarity in *Carex polymorpha*. We compared fecundity and seed set with a common species, *C. vestita* Willd. (section *Carex*). Although not phylogenetically closely related, *C. vestita* is morphologically similar, occurs sympatrically, and provides a useful congeneric comparison to test hypotheses on the causes of rarity of *C. polymorpha*.

MATERIALS AND METHODS

Study Sites

Studies of *Carex polymorpha* were conducted in three populations. Two were located in Falmouth Foreside, Cumberland County, Maine: the Borrow Pit site, an extensive area of former sand and gravel excavations with several vegetation types, and the Woods site, less than 2 km north of the Borrow Pit site, wooded and undisturbed. The third population was located in Duxbury, Plymouth County, Massachusetts, and grew on sand dikes of a former cranberry bog and in adjacent woods.

Comparative studies of *Carex vestita* were conducted at a population which grew in a power line right-of-way adjacent to a cemetery in Stoughton, Norfolk County, Massachusetts.

Flowering Phenology

Each site was visited weekly in May, 1988 to collect data on flowering phenology. The number of flowering shoots in each of five classes was recorded. These classes were defined as 1) not yet in flower, 2) in a female-only phase defined as having the stigmas white and exserted, 3) in a hermaphroditic phase defined as having both stigmas and anthers exserted, 4) in a male-only phase defined

as having anthers dehiscing and stigmas brown and withered, and 5) flowering shoots that had ceased to flower. Additional observations were made at the Borrow Pit site to assess numbers of flowering and vegetative shoots in consecutive 20-cm wide \times 100-cm long quadrats along three parallel transects. Each of these transects included areas of sand-vegetation edge, lightly shaded woods, and open sedge-dominated areas.

Fecundity

Female flower production (potential fecundity) was studied by counting the number of pistillate spikes and perigynia produced per flowering culm. For *Carex polymorpha*, 250 flowering culms were collected in mid-July 1988 from three subpopulations of the Maine Borrow Pit population. Of these, 50 culms were collected as a grab sample from an area in full sun (area 1), 100 from young woods collected along two 10-m transects (area 2), and 100 culms from the edge of a bog (area 3). For *C. vestita*, 100 culms were collected from a population along a utility line easement in Stoughton, Massachusetts. Seed set (actual fecundity) in both species was assessed by determining the number of mature achenes per flowering shoot. Percent seed set was calculated as the percent of perigynia containing mature achenes.

Breeding System

The breeding system of *Carex polymorpha* was investigated through experimental manipulation of plants at the Borrow Pit site in May, 1989. The subpopulation selected occurs in an open, relatively unshaded site where seed set would be expected to be high. This experiment was designed to determine whether the low seed set observed in 1988 was due to either self-incompatibility or to limited pollen dispersal in wooded sites.

Six treatments were used: 1) emasculated, 2) emasculated and bagged, 3) bagged, 4) emasculated, hand-pollinated with pollen from a different subpopulation, and bagged, 5) hand-pollinated with pollen from the same subpopulation, and 6) undisturbed controls. These treatments enabled us to determine whether plants were apomictic, self-compatible, or self-incompatible, and to isolate any effects due to emasculation or bagging. Ten replicates of each treatment were used. All pollinations were done on 21 May 1989, and bags were removed ten days later, after pollen release

in the population had ceased, to allow normal achene development. The unequal number of replicates analyzed in the results is due to the death of some shoots due to grazing or manipulation. Plants were emasculated by manual removal of the terminal staminate spike or spikes prior to emergence of stigmas, and were bagged by enclosure of the entire flowering culm, prior to emergence of stigmas, in glassine photographic negative envelopes (3 cm × 17 cm) which were tied at the base. Hand-pollination was accomplished by removal of a staminate spike with dehiscent anthers from a donor plant, and brushing the anthers of this spike onto the exposed stigmas of the receptor plant until the stigmas were visibly yellow. All the experimental culms were harvested on 13 July 1989, and the total numbers of perigynia and mature achenes were determined.

Vegetative Morphology

Destructive sampling of rhizomes was performed at the two Maine sites in six 1 m² quadrats: two in the Falmouth Woods population designated Woods 1 and 2, three along the sand-vegetation edge at the Borrow Pit site designated Borrow Pit A 1, 2 and 3, and one in a partially wooded area of the Borrow Pit site with a dense herbaceous layer of *Carex polymorpha* designated Borrow Pit B. The purpose was to investigate patterns of rhizome growth and shoot production. Data recorded for each inter-shoot unit (consisting of one to several internodes between scale-leaves) included the length of the unit and dry weight per cm of the rhizome. Data recorded for each node included the number of meristems produced and the developmental fate of each meristem (vegetative shoot, flowering shoot, rhizome). Rhizome weight was determined for arbitrarily selected 20 mm lengths of excavated rhizomes cut distally to the terminal living shoot, dried at 60°C for 24 hours, and weighed to the nearest .0001 gram.

Vegetative morphology was examined by measuring lengths and widths of the longest leaf from arbitrarily selected shoots in the Woods and Borrow Pit populations in Maine to determine whether canopy cover affects above-ground biomass production.

Permanent Plots

Shoot turnover was investigated in permanent plots established at randomly selected intervals along a line transect through the

longest axis of each population or subpopulation. Each permanent plot was 20 cm × 50 cm (.1 m²) and marked at the four corners by bamboo stakes inserted into the substrate. A mapping frame with a transparent acrylic top and adjustable hanging plumb line was used to record shoot locations, with an accuracy of ±1 cm. Shoot locations were mapped in May, July, and September (the early, middle, and late growing season) in 1988 and 1989 for the Maine populations. Permanent plots in the Massachusetts population were sampled in May, July and September 1988 and May 1989. These data were used to determine recruitment and turnover rates of vegetative shoots within and between growing seasons in different microhabitats.

Six permanent plots were established at the Borrow Pit population, three each along two transects. One transect was placed at the boundary between open sand and a vegetated area (transect A), and all plants were growing in sand. The second transect was placed in an area with an open canopy (transect B) and a dense herbaceous layer dominated by *Carex polymorpha*. Three permanent plots were established along a transect in the Woods population. Nine permanent plots were established at the Duxbury, Massachusetts site. Three plots were located along a transect on the top of a dike (transect A), three plots were in an area with an open canopy and a dense herbaceous layer dominated by *C. polymorpha* (transect B), and three plots were located in pine forest with a dense canopy (transect C).

Canopy Cover

Photographs were taken of the canopy by placing a camera with a 28 mm wide-angle lens at 10 cm above the ground, facing upwards. Photographs were taken when the canopy was fully expanded, on 8 July 1988 in Maine and on 15 July 1988 in Massachusetts. A matrix of 100 evenly-spaced dots was placed on each photograph to estimate the percent of canopy cover, which is correlated with light levels (Piper, 1989). At the Borrow Pit site, photographs of the canopy were taken within and at the edge of a partially wooded area dominated by *Carex polymorpha*. At the Falmouth Woods site, photographs were taken at several locations within the population. At the Duxbury site, photos were taken in the wooded areas where only vegetative shoots were present as well as in the open areas at the foot of the dike and

along the dike trail where both vegetative and flowering shoots were present.

RESULTS

Reproductive Biology

Flowering shoots comprise, on average, 1.5% of the total population of shoots in the Borrow Pit subpopulation sampled. Based on our observations, this figure is typical of populations in open or slightly shaded sites. In sites with a well-developed canopy, such as the Falmouth Woods site, flowering shoots comprise less than 1% of the total. In heavily shaded sites, such as portions of the Duxbury site, no flowering shoots may develop.

Plants of *Carex polymorpha* are protogynous. For an individual shoot, the initial pistillate phase has a duration of less than a week, the intermediate hermaphroditic phase has a duration of one to two days, and the terminal staminate phase lasts from one to several days. Although dichogamous, the overlap in flowering potentially permits self-pollination to occur.

Plants within and among populations exhibit considerable asynchrony in flowering. At the Maine sites, the Borrow Pit population initiated flowering earlier than the Woods population. The Borrow Pit population was predominantly in the hermaphroditic phase on 16 May 1988, at which date the Woods population had not begun to flower. A week later, on 24 May, flowering shoots at the Borrow Pit had ceased flowering or were in their terminal staminate stage while all shoots at the Woods population were in a staminate phase. This Woods population showed a high degree of synchrony and completed the entire flowering sequence in 8 days. At the Massachusetts population, flowering of different subpopulations was also asynchronous, and flowering occurred over a 12-day period from 8–19 May. Achenes were mature in both Maine and Massachusetts populations by 23 July, approximately eight weeks after flowering had ceased.

The number of pistillate spikes, as well as the number of perigynia produced per flowering shoot, varied among subpopulations of *Carex polymorpha* at the Borrow Pit site: shoots in area 3 had, at most, one pistillate spike and on average 16 perigynia per spike, while shoots in areas 1 and 2 had at least one pistillate spike and on average 32–40 perigynia per shoot (Table 1). This difference

Table 1. Female flower and fruit production of *Carex polymorpha* and *C. vestita* (data are the mean \pm 1 SD).

Population	No. Pistillate		No. Achenes	% Seed Set
	Spikes	No. Perigynia		
Borrow Pit (1)	1.3 \pm 0.4	40.1 \pm 17.0	30.1 \pm 15.5	72.7 \pm 20.8
Borrow Pit (2)	1.4 \pm 0.5	32.1 \pm 11.7*	1.2 \pm 1.7*	4.5 \pm 6.4
Borrow Pit (3)	1.0 \pm 0.0	16.3 \pm 7.1*	1.2 \pm 1.9*	7.4 \pm 0.1
<i>C. vestita</i>	1.9 \pm 0.7	94.4 \pm 37.5	6.4 \pm 6.3	6.8 \pm 6.2

* Means are not significantly different at $P < .1$ in Student's t comparisons; all other means were significantly different.

among subpopulations in potential fecundity appears to be correlated with shading and canopy closure. Shoots of *C. vestita* tended to have two pistillate spikes and, on average, 95 perigynia (Table 1).

Actual fecundity, measured as the number of achenes and the percentage of perigynia which produced mature achenes, varied significantly among subpopulations of *Carex polymorpha* and between the two species (Table 1). The open, relatively unshaded subpopulation 1 of *C. polymorpha* at the Borrow Pit site had a seed set of 72% and produced on average 30 achenes per pistillate spike. This number is significantly different from the two more shaded Maine subpopulations (2, 3), which produced fewer than two achenes per spike and had seed sets of less than 10%. All populations of *C. polymorpha* differed significantly from *C. vestita*, which produced from 0–25 mature achenes per flowering shoot with an average seed set of less than 7%.

Mature achenes were obtained in all experimental pollination treatments (Table 2). The highest percent seed set was observed

Table 2. Achene production in breeding system experiment (mean \pm 1 SD). (See text for further explanation.)

Treatment*	n	Perigynia	Achenes	% Seed Set
1	9	52 \pm 25	42 \pm 22	78%
2	8	58 \pm 20	14 \pm 13	30%
3	7	43 \pm 17	22 \pm 10	55%
4	9	55 \pm 18	34 \pm 13	62%
5	7	44 \pm 18	31 \pm 18	70%
6	7	46 \pm 22	37 \pm 17	79%

* 1 = emasculated, open-pollinated; 2 = emasculated and bagged; 3 = selfed (bagged); 4 = outcrossed (emasculated, hand-pollinated, bagged); 5 = hand-pollinated (emasculated, hand-pollinated); 6 = control.

for the open-pollinated plants in treatments 1, 5 and 6. These seed set rates (> 70%) are comparable to those found for plants in open habitats, demonstrating that emasculation or hand-pollination have no discernable effects on seed set. The somewhat lower seed set figures for treatments 3 and 4 show no difference between donor pollen from the same plant or a different clone, but suggest that seed set was somewhat limited by bagging. The low seed set for treatment 2, in which plants were expected to set no seed if sexual and to have a significant seed set if apomictic, is puzzling. However, we found that although spikes are fundamentally unisexual, the majority of pistillate spikes developed a few inconspicuous staminate flowers at their tip which were not noticed and therefore not removed by emasculation. The presence of some pollen within the pollen exclusion bags in treatment 2 from these few anthers could explain the low level of seed set in this treatment testing for apomixis. This experiment for apomixis is thus not conclusive, but results are consistent with the hypothesis that *Carex polymorpha* is self-compatible and not apomictic.

Vegetative Morphology

Growth in the clonal species *Carex polymorpha* is sympodial, and occurs in the following sequence. The apical meristem of a rhizome turns upward and develops into a vegetative shoot which persists for a single growing season. During the growing season, axillary meristems form at the base of this shoot; these meristems may develop into elongate rhizomes which initiate further vegetative spread, or may develop into short ascending rhizomes which form either vegetative or flowering shoots. Individual leafy shoots persist for only a single growing season. This form of sympodial growth produces a pattern of either single, isolated shoots if all meristem growth is of elongate rhizomes, or may produce a pattern of tightly clustered shoots if most meristem growth is of short, ascending rhizomes.

The pattern of rhizome growth was investigated in the 6 quadrats that were excavated. By tracing rhizomes for their entire length in these quadrats, we found that relatively few shoots in any given square meter belonged to the same clone. Rhizomes are capable of continued growth for several meters, and rhizomes from several different directions converge and intermingle in a

Table 3. Comparison of rhizome inter-shoot unit lengths and meristem number among samples of *Carex polymorpha* in Maine.

Site	Quad-rat	<i>n</i>	Mean Rhizome Length (cm) ± SEM	Mean Number of Meristems	Canopy Cover
Woods	1	144	5.078 ^c ± 0.484	1.243 ^b	closed
	2	370	6.304 ^c ± 0.389	1.372 ^b	closed
Borrow Pit A	1	22	13.855 ^{a,b} ± 2.445	1.567 ^b	open
	2	38	15.850 ^a ± 1.752	2.721 ^a	open
	3	86	11.506 ^b ± 1.418	2.372 ^a	open
Borrow Pit B	1	74	3.920 ^c ± 0.393	1.107 ^b	closed

^{a,b,c} Differences between means were assessed using Student-Newman-Keul's *a posteriori* test in an ANOVA of comparisons by site. Differences among means with different group letters were significant at $P < .0001$. Means with the same letter were not significantly different. SEM = standard error of the mean.

single area. This growth pattern indicates that competition among different genets may be occurring at a high level in populations of *Carex polymorpha* that consist of more than one genet. Intact rhizome systems were excavated that had up to 14 nodes. Analysis of the branching pattern, based on our observations regarding shoot growth and differentiation, indicate that ramets may remain connected to the parent rhizome for at least 8, and perhaps as long as 10 years, based on the observation that a single node is produced per year at this site.

Rhizome inter-shoot unit lengths differed significantly among these sites (Table 3) and when sites were grouped according to canopy types. Rhizome inter-shoot lengths in the Woods and Borrow Pit B quadrats averaged 4–6 cm, but reached 11–14 cm in an open sand quadrat at the Borrow Pit site. Average inter-shoot length in closed canopy sites is 5.70 cm, while average internode length in open canopy sites is 12.99 cm. Analysis of variance showed this difference to be significant at $P < .0001$, $F = 92.68$.

The weights of rhizome segments differed between the Woods and Borrow Pit sand quadrats. The average rhizome dry weight (2 cm segment) for plants in the Borrow Pit quadrat was .0755 g, while average weight from plants in the Woods site was .0407 g. Student's *t*-test ($df = 44$) found this difference to be significant at $P < .1$, $t = 1.7939$ (the lower significance level of $P = .1$ was chosen due to the restricted amount of material available).

Leaf production and dimensions were studied in arbitrarily selected vegetative shoots from closed-canopy (Woods) and open (Borrow Pit) sites. Although there was some difference in the mean leaf number (Borrow Pit = 8.57 ± 1.94 , $n = 21$; Woods = 6.95 ± 1.09 , $n = 22$), the means were not significantly different according to Student's t -test ($t = .652$, $P < .1$). Lengths of the longest leaf of each shoot were also compared. Mean leaf lengths were somewhat different (Borrow Pit = 478.7 ± 80.7 mm, Woods = 430.3 ± 64.1 cm), but not significantly so ($t = .336$, $P < .1$). Leaf widths are significantly different between the shaded Woods and open Borrow Pit sites, with the Woods population having leaves on average $2.45 \pm .72$ mm wide, and the Borrow Pit population leaves 5.41 ± 1.12 mm wide ($t = 2.227$, $P < .05$). The narrower leaf width in the shaded site may result from limited resources available to support vegetative growth.

The average number of meristems produced per node was greater for plants growing in open sites ($\bar{x} = 2.31$, range 0–9) than in closed-canopy sites ($\bar{x} = 1.31$, range 0–5) based on an analysis of variance ($F = 59.12$, $P < .0001$). However, there were significant variations within the open sand site (BP-B), in which one replicate quadrat was found to be more similar to the Woods site. This variability may indicate that the open sandy quadrats were not located in a homogeneous environment, or may indicate that canopy effects are not the sole explanation for differences in rhizome meristem production.

Permanent Plots

Density of shoots in the permanent plots was correlated with canopy cover. Those plots with high shoot density (≥ 200 shoots/m²) were the Borrow Pit transect B (BP plots 4–6) and the similar Duxbury transect B (Table 4). These relatively unshaded sites had shoot densities ranging from 170 to 390 shoots/m². Two sets of plots, the Duxbury dike transect A and Falmouth Woods, were in more shaded areas and had intermediate shoot densities (100 to 200 shoots per m²). Two sites had very low shoot densities (< 100 shoots/m²). Duxbury transect C occurred in heavily shaded woods. Borrow Pit transect A (BP plots 1–3) was comparable to the intermediate density sites in shading, but occurred in a microsite with very sandy soil of potentially lower quality to plant growth due to lower water and/or nutrient availability.

Shoot turnover in the permanent plots, measured as the rate of persistence of individual shoots during a growing season, appeared to be correlated to canopy closure. In the forested sites (Falmouth Woods, Duxbury C) nearly all shoots present at the beginning of a growing season persisted through the season, and few or no new shoots were initiated (Table 4). Shoot density is lowest in these populations as well. Several plots (Borrow Pit 4–6, Duxbury B) had high rates of shoot turnover, with as little as 50% of the total shoot population persisting through a growing season (Table 4). The total shoot number in each of these plots tended to remain approximately the same at each sampling date as well as throughout the growing season despite turnover of 20–40% of the shoots; it is clear that these sites with high turnover also had the highest shoot density.

Most sites and plots exhibited little change in total number of shoots from year to year, although minor fluctuations were common. Three plots, Duxbury A-1, Borrow Pit 1 and 2 showed increases of up to 100% from year 1 to year 2 of the study (Table 4). One plot, Borrow Pit 3, showed a decline of 50% in this period. These data indicate that the vegetation-sand edge is a very dynamic region, in which the population may expand rapidly, suffer high levels of shoot mortality, or both.

Canopy Cover

Results from the measurement of canopy closure are not sufficiently precise, nor were a sufficient number of replicate measurements taken to provide adequate statistical precision to their analysis. The two populations with substantial numbers of flowering shoots (Borrow Pit B and Duxbury A) had, on average, less than 50% canopy cover above patches of flowering shoots: at the Borrow Pit, the median was 42% (range 9–69%); at Duxbury the median was 30% (range 15–65%). Areas within these populations where only vegetative shoots were present had substantially higher canopy cover, with median values above 80%. Two populations which had low levels of flowering, Falmouth Woods and Duxbury B, had canopy cover of approximately 65–80% above both flowering shoots and vegetative shoots. The population that had no flowering, Duxbury C, had a median canopy cover of 82%.

A correlation between canopy cover and flowering frequency is strongly suggested. Canopy cover of less than 50% appears to

Table 4. Within-year shoot turnover* and changes in shoot numbers for *Carex polymorpha*.

Quadrat		Date						Annual Turnover
		5/88	7/88	9/88	5/89	7/89	9/89	
Duxbury A-1	Shoot number	4	6	5	16	—	—	+120
	% Turnover	—	0	33	—	—	—	
	% Change	—	+50	-16	—	—	—	
A-2	Shoot number	24	25	26	24	—	—	0
	% Turnover	—	8	48	—	—	—	
	% Change	—	+4	+4	—	—	—	
A-3	Shoot number	16	18	15	16	—	—	0
	% Turnover	—	0	17	—	—	—	
	% Change	—	+13	-17	—	—	—	
B-1	Shoot number	38	27	37	34	—	—	-40
	% Turnover	—	58	7	—	—	—	
	% Change	—	-29	+37	—	—	—	
B-2	Shoot number	23	27	28	25	—	—	+20
	% Turnover	—	39	7	—	—	—	
	% Change	—	+17	+4	—	—	—	
B-3	Shoot number	36	37	37	39	—	—	+30
	% Turnover	—	8	16	—	—	—	
	% Change	—	+3	0	—	—	—	
C-1	Shoot number	4	4	4	4	—	—	0
	% Turnover	—	0	0	—	—	—	
	% Change	—	0	0	—	—	—	
C-2	Shoot number	4	4	5	5	—	—	+10
	% Turnover	—	0	0	—	—	—	
	% Change	—	0	+25	—	—	—	

Table 4. Continued.

Quadrat		Date						Annual Turnover
		5/88	7/88	9/88	5/89	7/89	9/89	
C-3	Shoot number	4	5	5	3	—	—	—10
	% Turnover	—	0	20	—	—	—	
	% Change	—	+25	0	—	—	—	
Maine** BP-1	Shoot number	10	10	11	8	8	6	
	% Turnover	—	0	0	—	0	25	
	% Change	—	0	+10	—	0	—25	
BP-2	Total shoots	2	2	2	5	7	6	
	% Turnover	—	0	0	—	0	14	
	% Change	—	0	0	—	+40	—14	
BP-3	Total shoots	4	4	4	6	6	5	
	% Turnover	—	0	0	—	0	17	
	% Change	—	0	0	—	0	—17	
BP-4	Total shoots	19	17	18	17	24	20	
	% Turnover	—	11	0	—	0	21	
	% Change	—	—11	+6	—	+42	—17	
BP-5	Total shoots	32	31	28	26	32	27	
	% Turnover	—	38	29	—	0	22	
	% Change	—	—3	—10	—	+23	—16	
BP-6	Total shoots	19	17	17	13	13	13	
	% Turnover	—	11	18	—	0	8	
	% Change	—	—11	0	—	0	0	

Table 4. Continued.

Quadrat		Date						Annual Turnover
		5/88	7/88	9/88	5/89	7/89	9/89	
FW-1	Total shoots	19	14	12	13	14	—	
	% Turnover	—	26	36	—	0	—	
	% Change	—	-26	-14	—	+8	—	
FW-2	Total shoots	10	11	12	12	12	9	
	% Turnover	—	0	0	—	0	25	
	% Change	—	+10	+9	—	0	-25	
FW-3	Total shoots	6	6	4	5	5	5	
	% Turnover	—	17	33	—	0	0	
	% Change	—	0	-33	—	0	0	

* Percent turnover is calculated as number of shoots persisting between sampling dates divided by the total number of shoots on the previous sampling date. Percent change is calculated as the difference in total shoot number on two successive sampling dates, divided by the total number of shoots on the earlier sampling date.

** BP = Borrow Pit; FW = Falmouth Woods.

promote flowering, while the canopy cover between 50 and 80% inhibits flowering, although environmental factors other than light may be important in regulation of flowering within this range of light levels. Canopy cover greater than 80% appears to inhibit flowering completely.

DISCUSSION

Sexual reproduction in *Carex polymorpha* is potentially resource-limited at each stage of reproduction. Production of flowering shoots may be initially limited primarily by light levels which reduce allocation of resources to flowering. Light, measured by canopy closure, further limits the number of pistillate spikes and perigynia produced by each flowering shoot. Finally, resources may limit the number of achenes which mature. The net result is lack of sexual reproduction in severely shaded habitats, negligible seed set in less shaded sites, and high levels of seed set only in the most open sites.

Flowering shoots form, on average, 1.5% of the total population of shoots. Based on our observations, this ratio is typical of populations in favorable conditions such as open or slightly shaded sites. In sites with a well-developed canopy, flowering shoots form less than 1% of the population, or may be entirely absent. Piper (1989) found that microsite variation in light had a strong influence on flowering in *Smilacina*, due to the increase in shoot size with increased light.

This correlation between canopy cover and flowering frequency is supported by our study of canopy closure. The highest incidence of flowering in *Carex polymorpha* occurred where the canopy cover was less than 50%, and decreased to zero in areas where the canopy cover was greater than 80%.

In populations with high numbers of flowering shoots, reproductive success may be limited by the number of pistillate spikes and the number of perigynia produced per flowering shoot. Differences among subpopulations in potential fecundity (the number of female flowers produced) also appeared to be correlated with shading and canopy closure, with the highest potential fecundity in the most open sites.

Reproduction is further limited by seed-set. Although the number of perigynia determines potential fecundity, actual fecundity is measured as the number of achenes which mature, and ranges

from 72% in open areas to less than 10% in areas with higher canopy cover. These figures are comparable to the average fruit-set for self-compatible monoecious species, for herbaceous perennials, for temperate species, for species with "cheap fruits," and for wind-pollinated plants (Sutherland 1986). *Carex polymorpha* may be placed in all of these categories.

Seed set is not reduced because of self-incompatibility in *Carex polymorpha*. The controlled breeding experiment showed that seed set rates for hand-pollinated plants are comparable to those for open-pollinated plants in the most favorable open habitats. These results were not conclusive due to unexpected low levels of self-pollen available to bagged inflorescences, but support the hypothesis that *C. polymorpha* is self-compatible and not apomictic, and that in open habitats fecundity is not limited by pollen availability. These results indicate that the low actual fecundity appears to be due to embryo abortion controlled by extrinsic environmental factors, such as resource limitation. Based on experience with controlled crosses in other species of *Carex*, we expect that the perigynia would not expand and no early embryo development would take place in unpollinated perigynia. Since the majority of perigynia on open-pollinated plants in shaded sites were fully developed with aborted embryos, we assumed in this species that where seed set is low, embryos abort due to resource limitation in this species.

Resource limitation of sexual reproduction reduces the potential for establishment of new individuals within existing populations. If light is the limiting resource, existing populations in severely shaded or wooded sites are incapable of expansion by sexual reproduction. Recruitment of new individuals can only occur in those populations where light levels are sufficiently high to trigger the production of flowering shoots and to allow the plants to allocate sufficient resources to developing achenes. By extension, only those populations which occur in open sites can produce propagules which may disperse, colonize new sites, and establish new populations. Recruitment of new individuals by seed may be rare in *Carex* in general, particularly in established populations. Bernard (1975, 1976) reported that no seedlings of either *C. rostrata* Stokes or *C. lacustris* Willd. were seen in several years of study. Callaghan (1976) also never observed seedlings of *C. bigelowii* Torrey. Our observations, including those of the senior author over the past 15 years, confirm this.

Reproductive biology of *Carex polymorpha* is similar to that of a wide range of other species characterized as “stress-tolerant competitors” (Grime, 1979), and does not appear to be correlated with the distribution or frequency of this species. Many long-lived herbaceous perennials are capable of extensive vegetative growth, and allocate resources to sexual reproduction only under favorable environmental circumstances. This strategy allows plants to compete successfully in established sites for limited resources such as space, light, nutrients, or water.

Comparisons were made to the common *Carex vestita* to determine whether reproductive characteristics of *C. polymorpha* are correlated with its rarity. *Carex vestita* had a significantly higher potential fecundity but a lower seed set; on average, shoots produced fewer than 7 achenes, with an average seed set of 6.8%. This species, even in open, apparently favorable habitats, has an actual fecundity which is lower than that of *C. polymorpha* in similar favorable sites. Fritz-Sheridan (1988) found a similar result for the rare *Erythronium grandiflorum* Pursh var. *candidum* (Piper) Abrams in comparison to the common var. *grandiflorum*. These results indicate that, although sexual reproduction in *C. polymorpha* is resource limited, there is no real difference from common or widely distributed species. Reduced sexual reproduction, measured here by number of flowering shoots, potential and actual fecundity, does not appear to be a cause of rarity in *C. polymorpha*.

The mode of vegetative reproduction in *Carex polymorpha* is similar to that of most rhizomatous species of *Carex*. This species has a sympodial growth form, in which a module consists of a rhizome and a terminal shoot which produces roots at nodes and which has buds in the axils of basal scale-leaves. Rhizomes may be horizontal and long, or short and vertical. This growth form produces a pattern of clusters of connected shoots produced by short rhizomes, dispersed at the ends of long rhizome segments. This sympodial growth form is typical of most *Carex* species investigated (Kershaw, 1962; Bernard, 1975, 1976; Noble et al., 1979; Callaghan, 1976; Schmid, 1984; Bedford et al., 1988) as well as other monocots such as *Smilacina stellata* (L.) Desf., *S. racemosa* (L.) Desf., and *Streptopus roseus* Michx. (Antos, 1988; Piper, 1989), and was illustrated by Bernard (1975).

This growth pattern can be described as producing “K-selected genets” which are long-lived and produce large stands, but for

which new genets are infrequently formed. However, shoots can be described as “r-selected modules” (Schmid, 1984) which are short-lived and produced rapidly and continuously. This pattern may also conform to the “stress-tolerant competitor” model of Grime (1979). This growth form has many ecological advantages; the potential of clones to spread by vegetative growth into different microsites buffers clones against disturbance and death. Clones, or their fragments, have the potential to take advantage of different microsite conditions, and to distribute resources between more- and less-favorable microsites. Nutrients and/or photoassimilates may be translocated from ramets in high-quality microsites to lower-quality sites, and may even out the patchy distribution of resources in forested sites. Studies of several other *Carex* species (Kershaw, 1962; Bedford et al., 1988) also found that rhizomes from several genets converged in each apparent clump or tuft of shoots. This convergence is presumably due to the ability of rhizome growth and shoot production to respond to and exploit resource gradients. Noble et al. (1979) showed that nutrient levels were correlated with development of dormant buds into shoots, allowing genets to exploit favorable microsites.

Rhizome persistence, rhizome lengths, and shoot dynamics of *Carex polymorpha* are similar to those found in other species of *Carex*. Rhizome continuity among shoot systems has been estimated at 7 to 12 years (Callaghan, 1976; Noble et al., 1979). Although Bedford et al. (1988) found horizontal rhizomes up to 60 cm long in *C. lasiocarpa* Ehrh., Noble et al. (1979) found that plants in favorable conditions produced rhizomes 11–16 cm long, while plants in less favorable sites produced shorter rhizomes 5–7 cm long. These results correspond with results for *C. polymorpha*.

Noble et al. (1979) described five phases which could be observed in populations of *Carex arenaria* L. The juvenile phase, at the leading edge of the clone, had a low density; the adolescent phase consisted of high shoot density (near the carrying capacity), but of vegetative shoots only; the mature phases had a similar shoot density, but with abundant flowering shoots. In the senile and slack phases, shoot density declined. Similar phases can be described for *C. polymorpha*. The juvenile phases, at vegetation-sand boundaries, have a low shoot density as found for the Borrow Pit A permanent plots. The adolescent and mature phases, typified by the Borrow Pit B plots and by Duxbury A and B plots, have

high shoot densities and high levels of flowering. Senile phases, with reduced density and no flowering, are typified by the forested areas of the Duxbury C and Falmouth Woods populations.

Turnover of shoots in *Carex polymorpha* is similar to patterns of shoot demography found in other species of *Carex*. Most studies have found a continuous emergence of new ramets, and new shoots present at all sampling dates (Bernard, 1976; Noble et al., 1979; Bedford et al., 1988). These studies also found the number of shoots present at any one time were constant over the growing season, despite considerable turnover. Noble et al. (1979) found that the highest death rate of shoots occurred at the same time as the highest birth rate, as we found for *C. polymorpha*. He hypothesized that this correlation could be due to the production of new shoots causing the death of older shoots, or that the death of old shoots allows the growth of new shoots.

Shoot density and dynamics are correlated with habitat conditions; densities and turnover are correlated, with the highest turnover rates associated with the highest densities. Shoot density and dynamics can be useful in predicting the health and stage of the population. Maximum densities occur in the most favorable microsites, and represent the “adolescent” or “mature” phases of clonal growth according to the model of Noble et al. (1979). Low densities occur in the least favorable sites and “senile” phase of growth, and are correlated with very low shoot turnover rates. Callaghan (1976) suggested that shoot turnover and the number of shoots in a population correlated with habitat quality, and that both were higher in high-quality sites. Our data suggest that low densities also occur in the “juvenile” advancing edge of the population where they are correlated with high turnover rates.

Results and observations from this study of the population biology of *Carex polymorpha* should enable rare-species managers to make informed decisions regarding habitat management and long-term monitoring goals. We have found that *Carex polymorpha* appears to be somewhat tolerant of frequent, low-level disturbance, judging by its occurrence and even vigor on the edges of dirt roads, dikes, trails, railroad embankments and utility rights-of-way which are regularly cleared of at least some vegetation. Such disturbance may reduce the shading effects of taller vegetation.

It is likely that *Carex polymorpha* is adapted to, or has been characteristic of, habitats with frequent fires. The typical habitats

in which we have found *C. polymorpha* have sandy, low-nutrient soils and tend to become very dry in late summer. These are habitats which are susceptible to fire, and which have canopy species (oaks, pitch pine) known to be fire-tolerant. Fires would reduce density of the canopy and increase the amount of light available to *C. polymorpha* for growth and reproduction, and may function to remove the litter layer that may inhibit seed germination. The underground rhizomes and meristems of *C. polymorpha* could survive a cool ground-fire and rapidly re-sprout. This conjecture is partially supported by our observations of the vigorous re-growth of *C. vestita* following a grass fire at the study site, as well as the similarity of its reproductive biology to that of *C. polymorpha*.

The development of modern concepts of rarity was recently presented by Fiedler (1986) in a review of historic and recent literature. She discussed the "age and area" hypotheses, which argued that rare species were either young species not yet dispersed to their potential range, or old, relict species reduced to a few sites. The concept of competition became integrated into this hypothesis, and many have argued that rare species are unable to compete successfully and expand into new sites. Stebbins (1980) and others have concluded that rare species are represented by a single or few genotypes, biotypes, or ecotypes, and are poor competitors. It is clear as we investigate the biology, evolutionary and recent history, and demographic patterns of rare species, that there is no single explanation for rarity. Rabinowitz et al. (1986) recognized seven types of rare species based on distribution, habitat specificity, and population sizes. Although this system enables rare species to be classified, it is also clear that it is inadequate to explain the complexity of rarity, and the individualistic nature of rare species.

Carex polymorpha has a moderately broad geographic distribution, a somewhat restricted habitat specificity, and large population sizes. These characteristics place it between two of Rabinowitz's classes of rare species, those with a narrow geographic range, broad habitat range, and large population and those with a wide geographic range, narrow habitat specificity, and large populations. The first group is hypothesized to have substantial ecological plasticity and a wide tolerance for environmental variation, but limited dispersal abilities which restrict their movement into new sites (i.e., may be genetically variable but reproductively

limited). The second group is hypothesized to have already sampled a wide range of sites, and to have achieved successful colonization only on those rare, suitable patches (i.e., may be genetically depauperate but reproductively successful).

The geographic distribution of *Carex polymorpha* provides some support for membership in the latter group; that it has colonized sites from Maine to Virginia indicates that many other sites have probably been “sampled” by propagules which have not successfully established populations. However, we can identify no unique habitat requirements for this species. *Carex polymorpha* has been shown to consist of a large number of genotypes and ecotypes (Standley and Dudley, unpubl. data), and does not fit the model of a genetically depauperate rare species. In this paper, we examine the hypothesis that limited reproductive potential, resulting in a reduced ability to colonize new sites or successfully compete when established, is a cause of rarity in *C. polymorpha*.

Threats to *Carex polymorpha* are substantial. Fewer than 30 extant populations are known to occur. Although the locations of these are known to regulatory agencies and The Nature Conservancy, few state laws or regulations are available that provide protection to this rare species. *Carex polymorpha* generally grows in upland habitats or in buffer zones to wetlands—areas that are generally not protected from development by Federal or state wetland protection statutes. The sandy substrates preferred by this species have, and continue to be, altered by sand and gravel removal operations. Several populations occur on railroad or utility rights of way or easements where vegetation management through use of herbicides may pose a threat. Unless placed under protective ownership, all localities must be regarded as under severe risk of development or alteration that would eliminate habitat suitable for *C. polymorpha*. Even within protected areas, habitat management may be necessary to maintain optimal conditions for vegetative growth and sexual reproduction necessary for the long-term viability of this species.

ACKNOWLEDGMENTS

This study was funded by the Maine Chapter of the Nature Conservancy, the Natural Heritage and Endangered Species Program of the Commonwealth of Massachusetts, and the Department of Environmental Resources of the Commonwealth of

Pennsylvania. Barbara Vickery and Tom Rawinski provided valuable assistance and encouragement. We thank Robert Bertin, John Bernard, and two anonymous reviewers for their helpful comments on the manuscript.

LITERATURE CITED

- ANTOS, J. A. 1988. Underground morphology and habitat relationships of three pairs of forest herbs. *Amer. J. Bot.* 75: 106–113.
- BEDFORD, B. L., N. R. RAPPAPORT AND J. M. BERNARD. 1988. A life history of *Carex lasiocarpa* Ehrh. Ramets. *Aquatic Bot.* 30: 63–80.
- BERNARD, J. M. 1975. The life history of shoots of *Carex lacustris*. *Canad. J. Bot.* 53: 256–260.
- . 1976. The life history and population dynamics of shoots of *Carex rostrata*. *J. Ecol.* 64: 1045–1048.
- CALLAGHAN, T. V. 1976. Growth and population dynamics of *Carex bigelowii* in an alpine environment. *Oikos* 27: 402–413.
- FIEDLER, P. L. 1986. Concepts of rarity in vascular plant species, with special reference to the genus *Calochortus* Pursh (Liliaceae). *Taxon* 35: 502–518.
- FRITZ-SHERIDAN, J. K. 1988. Reproductive biology of *Erythronium grandiflorum* varieties *grandiflorum* and *candidum* (Liliaceae). *Amer. J. Bot.* 75: 1–14.
- GRIME, J. P. 1979. *Plant Strategies and Vegetation Processes*. John Wiley and Sons, New York.
- KERSHAW, K. A. 1962. Quantitative ecological studies from Landmannahellir, Iceland. III. Variation of performance in *Carex bigelowii*. *J. Ecol.* 50: 393–399.
- NOBLE, J. C., A. D. BELL AND J. L. HARPER. 1979. The population biology of plants with clonal growth. I. The morphology and structural demography of *Carex arenaria*. *J. Ecol.* 67: 983–1008.
- PIPER, J. K. 1989. Dispersal, establishment, and survivorship of a cohort of *Erythronium americanum*. *Bull. Torrey Bot. Club* 116: 247–257.
- RABINOWITZ, D., S. CAIRNS AND T. DILLON. 1986. Seven forms of rarity and their frequency in the flora of the British Isles, pp. 182–204. *In*: M. E. Soule, Ed., *Conservation Biology, The Science of Scarcity and Diversity*. Sinauer, Sunderland, MA.
- SCHMID, B. 1984. Life histories in clonal plants of the *Carex flava* group. *J. Ecol.* 72: 93–114.
- STEBBINS, G. L. 1980. Rarity of plant species: a synthetic viewpoint. *Rhodora* 82: 77–86.
- SUTHERLAND, S. 1986. Patterns of fruit-set: what controls fruit-flower ratios in plants? *Evolution* 40: 117–128.

L. A. S.

DAYLOR CONSULTING GROUP
SUITE 216
WORLD TRADE CENTER
BOSTON, MA 02210

J. L. D.

DEPARTMENT OF BIOLOGY
BOSTON UNIVERSITY
BOSTON, MA 02215